If you eat, I eat: resolution of sexual conflict over consumption from a shared resource

If you eat, I eat: resolution of sexual conflict over consumption from a shared resource

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Highlights

- We examined how parents resolve conflict over consumption of a shared resource
- We manipulated the parents' body size to create variation in food consumption
- Small parents consumed less food than large parents
- Each parent also adjusted its consumption based on attributes of its partner
- This new form of sexual conflict is resolved through matching and sealed bids

Abstract

Sexual conflict arises whenever males and females have divergent reproductive interests. The mechanisms mediating the resolution of sexual conflict have been studied extensively in the context of parental care, where each parent adjusts its decision about how much care to provide based on its partner's workload. However, there is currently no information on the mechanisms mediating the resolution of sexual conflict over personal consumption from a shared resource. We address this gap in the burying beetle *Nicrophorus vespilloides*, which breeds on small vertebrate carcasses. The carcass serves as a source of food for both the developing larvae and the caring parents, and parents feed from the carcass for self-maintenance. To study the mechanisms mediating conflict resolution, we experimentally varied the two parents' body size to create variation in carcass consumption. We then assessed whether each parent adjusted its consumption based on its own size, its partner's size, and its partner's consumption. As expected, large parents gained more mass than small parents. Furthermore, males paired to large females gained more mass than males paired to small females, and females responded to their partner's mass change, gaining more mass when their partner did. Our study provides insights into the resolution of a new form of sexual conflict, showing that it is mediated through both matching and sealed-bid responses. Our findings also suggest that the resolution models developed in the context of sexual conflict over biparental care may apply more generally than previously thought.

Keywords: breeding resource, burying beetle, matching, negotiation, sealed bids, sexual conflict, self-maintenance, somatic investment

Introduction

Sexual conflict arises whenever males and females have divergent reproductive interests and can occur in various contexts before mating (e.g. male harassment and female resistance; Arnqvist & Rowe, 2005), during mating (e.g. duration of copulation; Schneider et al., 2006), or after mating (e.g. contribution to parental care; Houston et al., 2005). Even though previous research has examined many types of sexual conflict (Arnqvist & Rowe, 2005; Houston et al., 2005; Parker, 2006), one type of conflict that so far has been neglected is that over the consumption of a food resource that is shared by the two parents and their offspring.

Sexual conflict over the consumption of a shared food resource might be common across animal taxa. For example, in many birds, the two parents share a breeding territory, within which each parent searches for food, some of which is used for its own consumption and some is used to provision its nestlings. Also, in many insects with biparental care, the two parents share resources in the form of dung, carrion, or wood that serve as food for the parents as well as the developing larvae (Tallamy & Wood, 1986). Each parent benefits personally by consuming from the shared resource, as it allows that parent to invest in self-maintenance and thereby enhance its future reproductive potential (Creighton et al., 2009; Billman et al., 2014). However, given that resources are finite, increased consumption by one parent leaves less of the resource for the offspring and the partner. A study on the burying beetle *Nicrophorus vespilloides* suggested that sexual conflict over shared resources during the breeding attempt may negatively affect female longevity (Boncoraglio & Kilner, 2012). Thus, there is evidence for a conflict battleground between the two sexes over personal consumption from the shared resource, with each parent preferring to consume more resources than would be optimal from its partner's perspective. Nevertheless, the mechanisms underlying the resolution of this form of conflict are still unexplored.

We suggest four mechanisms that might be involved in the resolution of sexual conflict over consumption from a shared resource. The first potential mechanism is coercion, which is based on physical aggression between the two parents. If coercion is mediating the resolution of this conflict, consumption of the resource should depend on asymmetries in fighting ability between the two parents, as the stronger parent might be in a position to control the feeding behaviour of its partner. The other three possible mechanisms (negotiation, matching, and sealed-bid decisions) derive from theoretical models for the resolution of sexual conflict over contribution towards parental care. Negotiation and matching occur when each parent adjusts its own contribution in direct response to its partner's contribution (McNamara et al., 1999; Johnstone & Hinde, 2006). When there is negotiation, the focal parent responds to a reduction in the amount of care provided by its partner by increasing its contribution (McNamara et al., 1999), while when there is matching, the focal parent matches any increase or reduction in its partner's contribution (Johnstone & Hinde, 2006). Sealed-bid decisions occur when each parent makes an initial fixed decision about how much to contribute that is independent of its partner's contribution (Houston & Davies, 1985). We suggest that these mechanisms might also apply to the resolution of sexual conflict over consumption from a shared resource because there are clear analogies between these two forms of conflict. Sexual conflict over contributions to parental care occurs because the benefits of care are shared between the two parents while the costs of care are personal (Lessells, 2012), whereas sexual conflict over consumption from a shared resource occurs because the costs of consumption are shared between the parents while the benefits of consumption are personal.

In this study, we investigate the mechanisms underlying the resolution of sexual conflict over carrion consumption in the burying beetle *N. vespilloides*, an insect that breeds on carcasses of small vertebrates (Eggert et al., 1998). The carcass serves as a source of food for

the two parents and their offspring during larval development, so the more each parent consumes from the resource, the less will be left for its partner and the offspring (Scott, 1989; Boncoraglio & Kilner, 2012). Previous work in the burying beetle *N. orbicollis* has shown that there is substantial variation in the parents' mass change over the breeding attempt and that this mass change is a proxy for investment in future reproduction (Creighton et al., 2009; Billman et al., 2014). Because we were interested in whether each parent adjusts its carrion consumption in response to that of its partner, we experimentally varied the body size of the two parents on the assumption that larger individuals consume more carrion. This asymmetry in body size inadvertently introduced asymmetry in the physical strength of the two parents (Otronen, 1988), allowing the possibility that the larger parent might enforce their feeding optimum by eating more while interfering with its partner's access to the carcass. Evidence for physical interference between partners has been observed in the closely related *N. defodiens*. In this species, females behave aggressively towards their male partner to prevent their partner from attracting additional females (Eggert & Sakaluk, 1995).

To study the mechanisms mediating conflict resolution and assess whether each parent adjusts its consumption based on its own size, its partner's size, and its partner's consumption, we recorded (*i*) the amount of time spent feeding on the carcass by each parent during a 30-min observation and (*ii*) the change in the mass of each parent over the reproductive attempt (Creighton et al., 2009; Billman et al., 2014). If the sexual conflict over carrion consumption is resolved through negotiation, we predicted that the focal parent would reduce its consumption in response to an increase in consumption by its partner. If it is resolved through matching, we predicted that the focal parent would increase its consumption in response to an increase in consumption by its partner. If the conflict is resolved through sealed-bid decisions, each parent's decisions about how much to consume should be independent of its partner's

consumption. Lastly, if the conflict is resolved through coercion, we predicted that the larger parent would prevent its smaller partner from consuming from the carcass.

Methods

General methodology

We used virgin beetles from an outbred laboratory population maintained at the University of Edinburgh. The beetles used in this study comprised of sixth-, seventh-, and eighth-generation beetles from lines originally collected in Edinburgh, UK and Warmond, The Netherlands. They were housed individually in transparent plastic containers (12×8×2 cm) filled with moist soil and kept at 20°C and constant light. Non-breeding adults were fed raw organic beef twice a week.

Experimental design

To induce variation in carcass consumption by the parents, we first generated small and large beetles using a full-sib design based on previously established methodology (Steiger, 2013; Pilakouta et al., 2015). For each of these 90 broods, we removed half of the brood from the carcass once the larvae reached the third instar, leaving the remaining larvae on the carcass until right before dispersal. We recorded the mass of each larva and kept the larvae in individual containers with moist soil. Larvae weighing less than 150 mg were categorised as small (mean ± SD: 111 ± 14 mg), while larvae weighing more than 150 mg were categorized as large (203 ± 24 mg). Larval mass at dispersal determines adult size, as larvae do not feed after dispersal from the carcass and before eclosion (Bartlett & Ashworth, 1988; Lock et al., 2004).

All beetles were bred within two weeks after sexual maturity (10-24 days after eclosion) using a 2×2 factorial design: a large male paired with a large female (N=25), a large male

paired with a small female (*N*=25), a small male paired with a large female (*N*=25), and a small male paired with a large female (*N*=25). Paired beetles were virgins and did not share common ancestors for at least two generations. The pairs were transferred to transparent plastic containers (17×12×6 cm) with moist soil and were provided with freshly thawed mouse carcasses (Livefoods Direct Ltd, Sheffield, UK) of a standardized size (22-25 g). For each of these matings, we recorded the mass of the carcass and the pre-breeding mass of each parent. Immediately after eggs were laid, we moved the parents and the carcass to a new container. When the eggs started hatching, we generated experimental broods of 15 larvae by pooling larvae from eggs across all treatments (Mattey & Smiseth, 2015). This design ensured that there was no parent-offspring co-adaptation (Lock et al., 2004) and that any differences in the parents' consumption of the carcass were not mediated through differences in brood size.

Twenty-four hours after providing the parents with a brood, we conducted behavioural observations using instantaneous sampling every 1 min for 30 min (Martin & Bateson, 1986; Smiseth & Moore, 2002; Smiseth et al., 2003). During this time, we recorded the number of scans that each parent spent feeding on the carcass. Parents were then allowed to care for the brood undisturbed until the larvae dispersed from the carcass about four days later. At dispersal, which corresponds to the end of the parental care period, we recorded the post-breeding mass of each parent. We calculated each parent's change in mass during the breeding period, by subtracting its pre-breeding mass from its post-breeding mass.

Statistical analyses

Data were analysed using R version 3.2.0. In all analyses for mass change, we used absolute rather than relative changes in mass, because we were specifically interested in examining differences in the amount of carrion consumed. Mass change data had a normal

error structure, so we used general linear models for those analyses. Because the behavioural data (time spent feeding on carcass) were zero-inflated, we ran zero-adjusted negative binomial (ZANB) regressions, using the hurdle function in the pscl package (Jackman, 2014), which splits the data into two components. Significant values on the zero-hurdle model indicate that a given variable influenced the probability of consuming carrion, whereas significant values on the count model indicate that a given variable influenced how much time was spent consuming carrion. All models included male size, female size, the interaction between male and female size, as well as time spent feeding or mass change by the partner. Previous studies on the same species investigating the resolution of sexual conflict over biparental care found that the focal parent's response to the partner's behaviour and the partner's state were independent (Mattey & Smiseth, 2015; Pilakouta et al., 2015), so we included both variables in our starting models. Note that in all models, the reference category for male and female size was 'large.'

Carcass size was included as a covariate in all models because resource availability may influence the parents' consumption. Males but not females spent more time feeding on larger carcasses (male: z=2.03, P=0.042; female: z=1.54, P=0.12), but carcass size had no effect on mass change in either sex (male: t=-0.70, P=0.48; female: t=-0.91, P=0.36). We also added brood size at the time of the observation as a factor, because although we provided all parents with a brood of 15 newly hatched larvae, there was some variation in the number of larvae alive at the time of the observation. Nevertheless, brood size did not have a significant effect on the amount of time parents spent feeding on the carcass (male: z=-1.89, P=0.059; female: z=-1.61, P=0.11) or the parents' change in mass (male: t=-0.78, P=0.44; female: t=-1.40, P=0.17).

Decisions about which variables to include in the final models were based on AIC model-selection criteria. We also tested for multicollinearity in all models by estimating variance

inflation factors using the vif function in the car package (Fox & Weisberg, 2011). The largest variance inflation factors were ≤3, indicating absence of multicollinearity.

Ethical note

Our study adheres to the ASAB/ABS Guidelines for the Use of Animals in Research, the legal requirements of the UK, as well as all institutional guidelines at The University of Edinburgh. None of the procedures used in this study had the potential to cause pain or distress.

Results

Do parents adjust consumption based on own size?

Large parents spent more time feeding from the carcass (Table 1, Figure 1) and also gained more mass over the reproductive attempt (Table 2, Figure 2) than small parents.

Do parents adjust consumption based on the partner's size?

Males spent more time feeding from the carcass and gained more mass when they were paired to a large female than when paired to a small female (Tables 1 and 2, Figures 1 and 2). However, there was no significant difference in the time spent feeding or mass change by females paired to large and small males (Tables 1 and 2, Figures 1 and 2).

Is there an effect of the interaction on consumption?

There was a significant effect of the interaction between male and female size on male feeding behaviour and mass change (Tables 1 and 2). This interaction effect reflected that large males spent more time feeding and gained more mass when paired to a large female, whereas small males spent a similar amount of time feeding and gained the same mass

regardless of the size of their partner (Figures 1 and 2). There was no significant effect of the interaction between male and female size on female mass change or feeding behaviour (Tables 1 and 2).

Do parents adjust own consumption based on partner's consumption?

Males were more likely to feed from the carcass when their partner was feeding less (zero-hurdle model: Estimate=-0.12, SE=0.05, z=-2.2, P=0.027), but males that fed from the carcass did not adjust the amount of time they spent feeding based on their partner's feeding behaviour (Table 1). Females did not adjust their feeding behaviour to that of their partner (zero-hurdle model: Estimate=-0.34, SE=0.19, z=-1.8, P=0.070; count model: Table 1). Lastly, females responded to their partner's mass change, gaining more mass when their partner gained more mass (Table 2). Males, on the other hand, did not adjust their mass change in response to that of their partner (Table 2).

Discussion

In this study, we examined the mechanisms that mediate the resolution of sexual conflict in a previously neglected context: conflict over personal consumption from a resource that is shared by the two parents and their dependent offspring. We found some evidence for sealed-bid decisions (i.e., decisions that are independent of the partner's behaviour) as parents of both sexes adjusted their consumption of carrion based on their own size, and males adjusted their consumption based on the size of their partner. We also found some evidence for matching as females gained more mass when their partner gained more mass. We found no evidence for size-dependent coercion, as parents did not feed less when paired to large partners. Our results therefore suggest that the resolution models developed in the context of

sexual conflict over biparental care may apply more generally than previously thought. We provide a more detailed discussion of our results below.

The main aim of our experimental design was to induce variation in the parents' consumption of carrion by experimentally varying the body size of the focal parent and its partner. As expected, large parents of both sexes consumed more carrion than small parents. This result confirms our initial assumption that large individuals need more food to replenish their energy reserves and also provides some evidence for sealed-bid decisions, whereby a parent's decision about how much to consume is independent of its partner's behaviour. An inadvertent consequence of this size manipulation was that we introduced asymmetry in the physical strength of the two parents (Otronen, 1988). However, we found no evidence that large parents used their physical superiority to prevent a small partner from feeding on the carcass. Our results thus do not support the hypothesis that size asymmetry between parents can influence the resolution of sexual conflict through coercion or punishment. The absence of coercion in this context might be due to its potential costs; attacking a partner that contributes towards providing care for the offspring may incur costs to the focal parent in terms of receiving less assistance from the partner in the future.

Another key finding in our study was that each parent adjusted its consumption of carrion based on attributes of its partner. Females gained more mass when their partner gained more mass, while males adjusted their mass gain based on their partner's body size rather than its consumption of carrion. These results suggest that there is a sex difference in how parents respond to attributes of their partner: females match their consumption to that of their partner as predicted by matching models (Johnstone & Hinde, 2006), while males make decisions that are independent of the behaviour of their partner as predicted by sealed-bid models (Houston & Davies, 1985). Previous work on the same species has reported sex differences in how caring parents respond to mate removal: males provide more care following the removal

247 of the female, while females provide a similar amount of care regardless of whether the male
248 is present or absent (Smiseth et al., 2005). The sex difference in personal consumption
249 reported here may reflect that females spend more time on the carcass than males (Smiseth &
250 Moore, 2004; Smiseth et al., 2005) and that females therefore have better access to
251 information about their partner's feeding rate. In contrast, males typically spend more time
252 away from the carcass and may adjust their mass change to the expected feeding rate of their
253 partner based on their partner's size. Indeed, we found that males spent more time feeding on
254 the carcass and gained more mass over the reproductive attempt when they were paired to a
255 large female, which consumed more carrion compared to a small female. The finding that
256 females match their consumption to that of their male partner is interesting given that there is
257 limited empirical evidence for matching in the context of biparental care (Hinde, 2006). Thus,
258 we suggest that the matching model (Johnstone & Hinde, 2006) might be better suited for the
259 resolution of sexual conflict over foraging from a shared resource.
260 For males, the observed pattern for feeding behaviour (Table 1) closely matched the
261 pattern for mass change over the reproductive attempt (Table 2); both male feeding behaviour
262 and male mass change were influenced by the male's own size, his partner’s size, and the
263 interaction between the two (Tables 1 and 2). In contrast, female mass change was influenced
264 by her own size and her partner's mass change (Table 2), but this pattern was not reflected in
265 the female's feeding behaviour (Table 1). One potential explanation for this sex difference is
266 that, when both parents provide care, females are typically much more involved in
267 provisioning food to the larvae than are males (Smiseth & Moore, 2004; Walling et al., 2008).
268 Thus, females may regurgitate most of the carrion they consume to the larvae, whereas males
269 may consume carrion primarily to replenish their own energy reserves. This interpretation is
270 supported by visual inspection of our data, which suggest that the overall mass change was
271 very similar for males and females in most treatments (Figure 2) even though females spent

significantly more time feeding on the carcass (Figure 1). An alternative explanation is that females appear to be spending more time feeding but instead they are making the carcass more accessible to the larvae. In this species, the larvae obtain some of their food by self-feeding from the day of hatching (Smiseth et al., 2003), and parents may enhance the larvae's ability to self-feed by cutting it open. It is not possible to discriminate between feeding and cutting the carcass open during behavioural observations. Another plausible explanation for the difference between the results for female feeding behaviour and mass change is that females incurred high energetic costs during egg production and laying, and they were consuming carrion to compensate for this initial energy cost. We cannot differentiate between these explanations based on the results from our experiment.

Overall, we found some evidence for sealed-bid decisions, as parents adjusted their consumption of carrion based on cues that were independent of their partner's behaviour: their own size (males and females) and their partner's size (males). However, we also found some evidence for matching, as females gained more mass when their partner gained more mass. The resolution of conflict over feeding from a shared resource is thus mediated through both matching and sealed-bid responses in this species. Interestingly, two recent papers in *N. vespilloides* showed that parents resolve conflict over parental care contributions using negotiation and sealed-bids (Mattey & Smiseth, 2015; Pilakouta et al., 2015). Our findings suggest that, even within the same species, different mechanisms may be involved in mediating the resolution of different forms of sexual conflict. We encourage future studies to explore whether this also might also be the case in other taxa.

Our results also raise interesting questions as to whether sexual conflict over consumption from a shared resource could influence sexual conflict over contributions to parental care. For example, if a parent is prevented from feeding by a physically superior partner, it may retaliate by providing less care. On the other hand, if a parent is providing a disproportionate

amount of care, its partner may be more tolerant of that parent feeding more from the resource. We are not aware of any studies investigating how the resolution of one type of sexual conflict may interact with the resolution of a different type of conflict in the same system. Such interactions might be expected whenever there are multiple types of sexual conflict occurring either simultaneously or sequentially over the reproductive bout, and we encourage future research to address this gap.

In summary, this study provides novel insights into the resolution of a largely ignored form of sexual conflict by showing that parents use information on their partner to decide how much food to consume from a shared resource. These adjustments in feeding are directly related to the parents' future reproductive potential, as consumption of the breeding resource is treated as a proxy for investment in future reproduction (Creighton et al., 2009; Billman et al., 2014). Our findings also suggest that parents use different mechanisms for the resolution of different forms of sexual conflict, and they raise the possibility of interactions between different sources of conflict occurring over the breeding attempt.

References

Arnqvist G., & Rowe, L. (2005). Sexual Conflict. Princeton University Press, Princeton, NJ.

Bartlett, J., & Ashworth, C. M. (1988). Brood size and fitness in *Nicrophorus vespilloides* (Coleoptera: Silphidae). *Behavioral Ecology and Sociobiology* 22, 429–434.

Billman, E. J., Creighton, J. C., & Belk, M. C. (2014). Prior experience affects allocation to current reproduction in a burying beetle. *Behavioral Ecology* 25, 813–818.

Boncoraglio ,G., & Kilner, R. M. (2012). Female burying beetles benefit from male desertion: sexual conflict and counter-adaptation over parental investment. *PLoS One* 7, e31713.

321 Creighton, J. C., Heflin, N. D., & Belk, M. C. (2009). Cost of reproduction, resource quality,
322 and terminal investment in a burying beetle. *American Naturalist* 174, 673–784.
323 Eggert, A-K., & Sakaluk, S.K. (1995). Female-enforced monogamy in burying beetles.
324 *Behavioral Ecology and Sociobiology* 37, 147–153.
325 Eggert, A.-K., Reinking, M., & Müller, J. K. (1998). Parental care improves offspring
326 survival and growth in burying beetles. *Animal Behaviour* 55, 97–107.
327 Fox, J., & Weisberg, S. (2011). An R Companion to Applied Regression, Second Edition.
328 Thousand Oaks, CA. URL: http://socserv.socsci.mcmaster.ca/jfox/Books/Companion
329 Hinde, C. A. (2006). Negotiation over offspring care?—a positive response to partner-
330 provisioning rate in great tits. *Behavioral Ecology* 17, 6–12.
331 Houston, A. I., & Davies, N. B. (1985). *The evolution of cooperation and life history in the*
332 *dunnock*, Prunella modularis. R. Sibly, R. Smith (Eds.), Behavioural Ecology: the
333 Ecological Consequences of Adaptive Behaviour, Blackwell Scientific Publications,
334 Oxford (1985), 471–487.
335 Houston, A. I., Székely, T., & McNamara, J. M. (2005). Conflict between parents over care.
336 *Trendsin Ecology and Evolution* 20, 33–38.
337 Jackman, S. (2014). *pscl: Classes and Methods for R Developed in the Political Science*
338 *Computational Laboratory*. Department of Political Science, Stanford University,
339 Stanford, California. R package version 1.4.6, http://pscl.stanford.edu/
340 Johnstone, R. A., & Hinde, C. A. (2006). Negotiation over offspring care–how should parents
341 respond to each other's effort? *Behavioral Ecology* 17, 818–827.
342 Lessells, C. M. (2012). Sexual conflict. In: *The Evolution of Parental Care* (N.J. Royle, P.T.
343 Smiseth & M. Kölliker, eds.), pp. 150–170. Oxford University Press, Oxford.
344 Lock, J. E, Smiseth, P. T., & Moore, A. J. (2004). Selection, inheritance, and the evolution of
345 parent-offspring interactions. *American Naturalist* 164, 13–24.

346 Martin, P., & Bateson, P. (1986). Measuring behaviour: an introductory guide. Cambridge
347 University Press.
348 Mattey, S. N., & Smiseth, P. T. (2015). Complex effects of inbreeding on biparental
349 cooperation. *Amerivan Naturalist* 185, 1–12.
350 McNamara, J. M., Gasson, C. E., & Houston, A. I. (1999). Incorporating rules for responding
351 into evolutionary games. *Nature* 401, 368–371.
352 Otronen, M. (1988). The effect of body size on the outcome of fights in burying beetles
353 (*Nicrophorus*). *Annales Zoologici Fennici* 25, 191–201.
354 Parker, G. A. (2006). Sexual conflict over mating and fertilization: an overview.
355 *Philosophical Transactions of the Royal Society B* 361, 235–259.
356 Pilakouta, N., Richardson, J., & Smiseth, P. T. (2015). State-dependent cooperation in
357 burying beetles: parents adjust their contribution towards care based on both their own
358 and their partner's size. Journal of Evolutionary Biology.
359 Schneider, J. M., Gilberg, S., Fromhage, L., & Uhl, G. (2006). Sexual conflict over
360 copulation duration in a cannibalistic spider. *Animal Behaviour* 71, 781–788.
361 Scott, M. P. (1989). Male parental care and reproductive success in the burying beetle,
362 *Nicrophorus orbicollis*. *Journal of Insect Behavior* 2, 133–137.
363 Smiseth, P. T., & Moore, A. J. (2002). Does resource availability affect offspring begging
364 and parental provisioning in a partially begging species? *Animal Behaviour* 63, 577–585.
365 Smiseth, P. T., & Moore, A. J. (2004). Behavioral dynamics between caring males and
366 females in a beetle with facultative biparental care. *Behavioral Ecology* 15, 621–628.
367 Smiseth, P. T., Darwell, C. T., & Moore, A. J. (2003). Partical begging: an empirical model
368 for the early evolution of offspring signalling. *Proceedings of the Royal Society of*
369 *London B* 270, 1773–1777.

Smiseth, P. T., Dawson, C., Varley, E., & Moore, A. J. (2005). How do caring parents respond to mate loss? Differential response by males and females. *Animal Behaviour* 69, 551–559.

Steiger, S. (2013). Bigger mothers are better mothers: disentangling size-related prenatal and postnatal maternal effects. *Proceedings of the Royal Society of London B* 280, 20131225.

Tallamy, D. W., & Wood, T. K. (1986). Convergence patterns in subsocial insects. *Annual Review of Entomology* 31, 360–390.

Walling, C. A., Stamper, C. E., Smiseth, P. T., & Moore, A. J. (2008). The quantitative genetics of sex differences in parenting. *Proceedings of the National Academy of Sciences of the United States of America* 105, 18430–18435.

Table 1. Effects on the amount of time spent feeding from the carcass by male (M) and female (F) parents during a 30-min observation.

	M size				F size				Interaction				Partner's feeding rate			
	Est	SE	*z*	*P*	Est	SE	*z*	*P*	Est	SE	*z*	*P*	Est	SE	*z*	*P*
M feeding	-1.2	0.5	-2.2	**0.028**	-1.6	0.6	-2.7	**0.006**	2.0	0.8	2.5	**0.011**	-0.001	0.1	-0.01	0.99
F feeding	-0.21	0.26	-0.8	0.43	-0.5	0.27	-1.9	0.058	-0.4	0.5	-0.7	0.47	-0.36	0.19	-1.9	0.054

Data were analyzed using ZANB regressions. For simplicity, we present the results for the count model (see text for zero-hurdle model results). We provide information on the parameter estimates (Est), standard errors (SE), test statistics (*z*-values), and *P*-values. Statistically significant *P*-values are indicated in bold.

Table 2. Effects on male (M) and female (F) mass change during breeding.

	M size				F size				Interaction				Partner's mass change			
	Est	SE	*t*	*P*	Est	SE	*t*	*P*	Est	SE	*t*	*P*	Est	SE	*t*	*P*
M mass change	-29	5.6	-5.2	**<0.0001**	-18	5.7	-3.2	**0.002**	21	7.9	2.7	**0.009**	0.13	0.10	1.4	0.17
F mass change	-5.1	5.1	-1.0	0.32	-28	4.6	-6.1	**<0.0001**	-3.1	9.5	-0.3	0.74	0.22	0.11	2.0	**0.047**

Data were analysed using general linear models. We provide information on the parameter estimates (Est), standard errors (SE), test statistics (*t*-values), and *P*-values. Statistically significant *P*-values are indicated in bold.

Figure Legends

Figure 1. Means (± SE) for amount of time spent feeding on the carcass (min) by small or large males (M: black bars) and small or large females (F: grey bars) during a 30-min observation.

Figure 2. Means (± SE) for mass change (mg) over the reproductive attempt for small or large males (M: black bars) and small or large females (F: grey bars).

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Figure 1

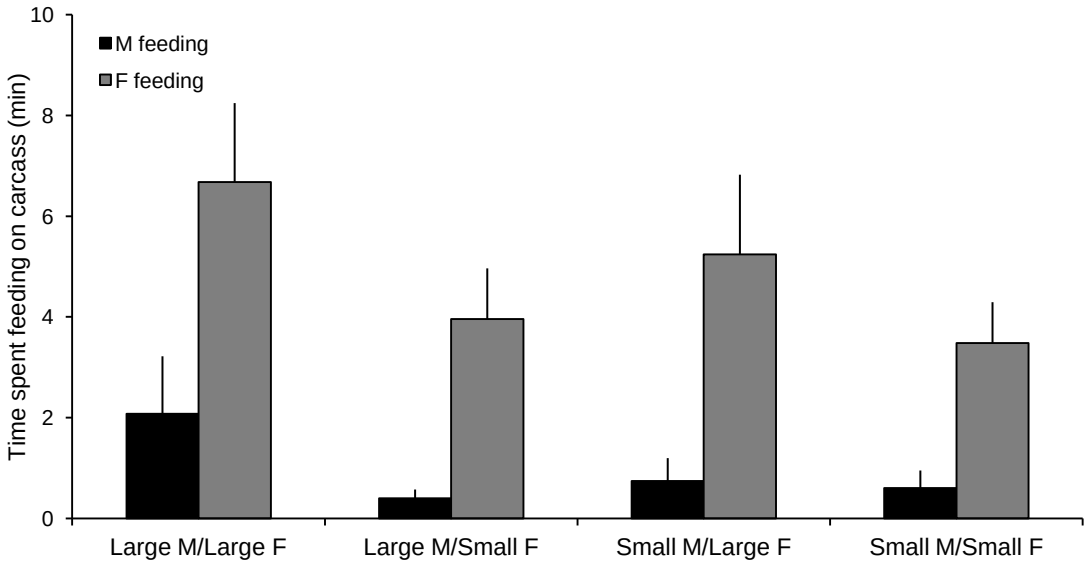
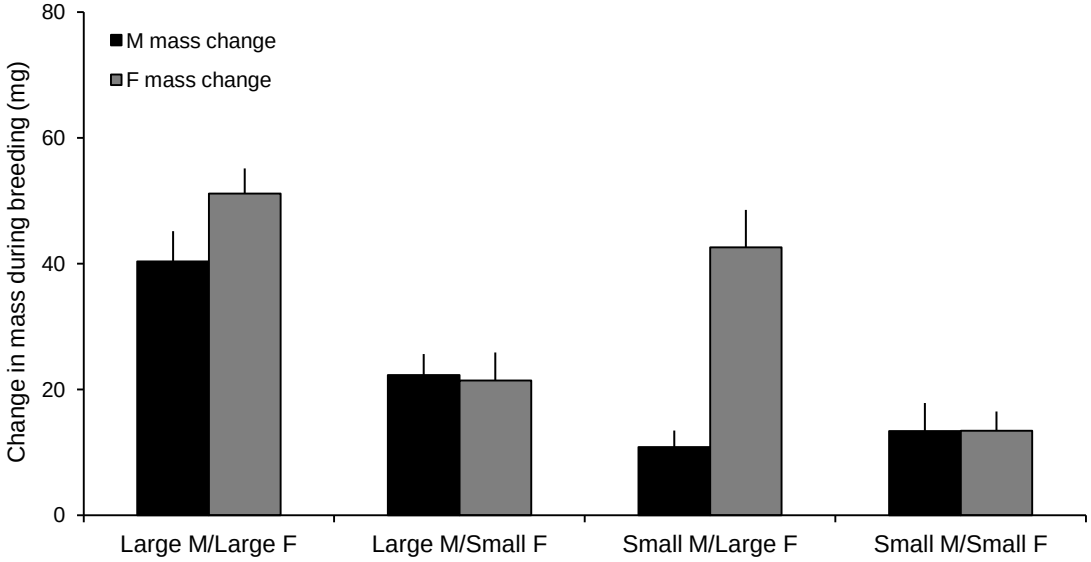

10
8
6
4
2
0
M feeding
F feeding
Time spent feeding on carcass (min)
Large M/Large F
Large M/Small F
Small M/Large F
Small M/Small F

Figure 2


80
60
40
20
0
M mass change
F mass change
Change in mass during breeding (mg)
Large M/Large F
Large M/Small F
Small M/Large F
Small M/Small F